THE AESTIVATION SITES OF BOGONG MOTHS, *AGROTIS INFUSA* (BOISDUVAL) (LEPIDOPTERA: NOCTUIDAE), IN THE SNOWY MOUNTAINS AND THE PROJECTED EFFECTS OF CLIMATE CHANGE.

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Abstract

Bogong moths constitute a keystone species in the ecology of the alpine zone of mainland Australia with an estimated 2.2 billion moths migrating to the Snowy Mountains annually. During spring they are found in temporary camps and in aestivation sites in boulderfields and among complex rock tors, with most moths moving to the higher altitude sites as summer progresses. Aestivation sites have a higher relative humidity than in nearby meteorological screens but similar temperatures. Crevices in boulderfields and among rock tors are open to heat exchange with the atmosphere during the summer and consequently their temperatures fluctuated in step with the fluctuations in the screens, but with the dampening of extremes in the aestivation sites. This meant that the average daily temperature in aestivation sites falls with increasing altitude at about 0.7°C per hundred metres of ascent, which approximates the regional lapse rate. As a consequence, questions about the future viability of aestivation sites for bogong moth populations (and that of their obligate parasites and predators) under a future climate change scenario can be answered from general climate models.

Introduction

Larvae of bogong moths Agrotis infusa (Noctuidae) feed in the western plains of eastern Australia from the Darling Downs in Queensland, south to the north-western plains of Victoria (Fig. 1). There is no regular monitoring of numbers of larvae despite their occasional outbreaks as pests, when they are believed to damage winter cereal crops (Gregg et al. 1994). The moth can be a univoltine or bivoltine species, with the cutworm larvae feeding on annual plants which are unavailable over summer. Because of this, most of the adults of the spring generation migrate to aestivate gregariously in the Australian Alps (Common 1954). The numbers of moths involved in this annual migration are not known, but Green (2010) calculated that total annual mortality of moths in the 1400 km² above 1500 m asl in the Snowy Mountains from predation, and non-predator-related causes such as parasitism and weather amounted to 1015 million moths. These contributed approximately 5000 GJ of energy annually together with 7 t of nitrogen and 1 t of phosphorus to the mountains, emphasising their importance as a keystone species in the ecology of the alpine zone.

A key to our understanding of the ecology of bogong moths in an uncertain climatic future is their summer distribution. Common (1954) tracked the changes in numbers at one site and recorded regularly used aestivation sites in the Brindabella Ranges. There are also a number of anecdotal records of locations and Common (1954) suggested that the frequency of the word 'bogong' in place names meant that sites where bogong moths congregated were likely to be quite common. The present study set out to examine the distribution of sites used by bogong moths in the Snowy Mountains above 1500 m asl (Fig. 2). This area is important because it contains the highest known sites and hence the ones least likely to be rendered unsuitable by climatic warming. A further aim was to examine the characteristics of sites to test their resilience in the face of future warming.

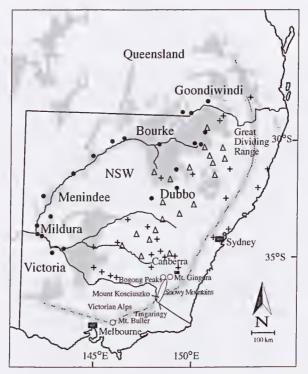
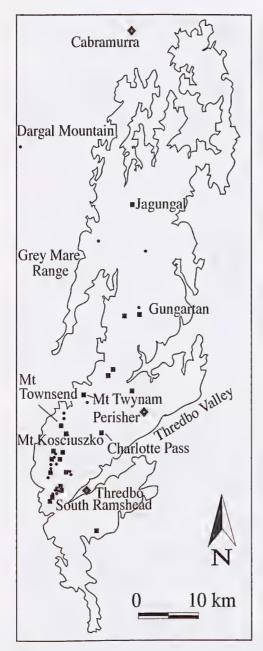


Fig. 1. Map of south-eastern Australia showing the self mulching soils (shaded) which are thought to be the important breeding areas for bogong moths, together with locations where larvae were collected by Froggatt (1900) (open triangles), Common (1954) (crosses), Green (2008) (closed circles), and the sites outside of the Snowy Mountains mentioned in the text. (After Common 1954).

Methods

Distribution of moths

In the summers of 2000/01 through to 2009/10, all large complex rocky outcrops, blockstreams and blockfields in the Snowy Mountains above 1500 m asl were searched for evidence of bogong moths. Sites were visited on foot with a final survey by helicopter to ensure that no obvious sites were missed. Sites in the present study were recorded as either an aestivation site used in



high summer or temporary camps, following the classification of Common (1954) of 'camps' and temporary camps. Locations of sites were recorded with a handheld GPS. The aspect of the aestivation crevices was recorded using a hand-held compass.

Statistical examination of the aspect was undertaken using the Rayleigh test (Batschelet 1981).

Movement of bogong moths out of temporary camps and into the higher aestivation sites is difficult to map because it is difficult for a person to observe inside most bogong moth sites. However, foxes are much smaller, and are driven by their need for food, so examination of their scats at different altitudes facilitated this monitoring. A study of fox diet on alpine and subalpine transects was under-taken from January 1996-December 1998 bv collecting scatsmonthly (Green 2003). The composition of scats was studied and the proportion of bogong moths present in them was determined for two complete

Fig. 2. Map of the contiguous area above 1500 m altitude in the Snowy Mountains showing moth aestivation sites (squares) and temporary camps (closed circles).

summer seasons, 1996/97 and 1997/98. These data were plotted to examine the relative abundance of bogong moths monthly at different altitudes.

Temperature and relative humidity

Temperature loggers and temperature/RH loggers (Tinytag plus and Tinytag Extra -Gemini Data Loggers, Chichester England) were deployed from 2001 onwards in a number of bogong moth camps and caves. Loggers were placed above ground level in free flowing air in areas where moths congregated. This was confirmed when moths were disturbed from behind the loggers at a number of sites when the loggers were retrieved.

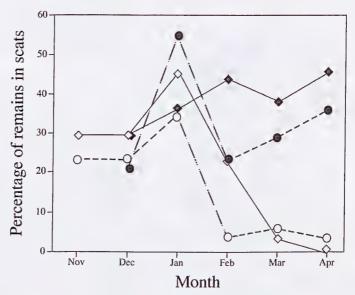


Fig. 3 Mean proportion of individual fox scats occupied by bogong moth remains at subalpine (open symbols) and alpine altitudes (closed symbols) over two summer seasons, 1996/97 (solid lines; diamonds) and 1997/98 (broken lines; circles).

Results

Distribution of moths

Within the study area in the Snowy Mountains there were 92 bogong moth temporary camps and 42 aestivation sites (Fig. 2). Outside the study area, bogong moth aestivation sites were found in isolated sites at Mt. Tingaringy $(37^{\circ} \ 00^{\circ}S. 148^{\circ} \ 40^{\circ}E)$ to the south-east of the Snowy Mountains on the Victorian Border, at the Bogong Mountains to the north-west, and on the peaks constituting the border with the Australian Capital Territory to the north east (Fig. 1), with a camp on Dargal Mountain (Fig 2). Most bogong moth sites were found along the highest ridge-line of the Kosciuszko Main Range, with a group of outliers around Gungartan and mainly individual

outliers elsewhere. Sites were generally complex rock tors or periglacial boulderfields and boulderstreams. Elsewhere, where rock outcropping was rare, for example to the north of Jagungal and southwest along the Grey Mare Range, there were no sites. The Crackenback Range, running along the northwestern side of the Thredbo Valley from east of Perisher Valley through to the South Ramshead contained outcroppings along the edge of the steep drop-off to the Thredbo Valley. Many of these outcroppings appeared suitable as aestivation sites or at least camps, but held no evidence of present or previous occupation by bogong moths.

The aspect of the aestivation sites was dependent upon geomorphology and the alignment of suitably exposed fragmented rock. For the test of preferred aspect, the relevant statistic for the Rayleigh test is w. If w > 3.0, then the null hypothesis of no clumping of bearings would be rejected. For the aestivation sites w = 0.138, and for the temporary camp sites w = 1.792. Thus both null hypotheses of no clumping were accepted. Because of the lack of clumping the calculation of mean bearing is meaningless.

No fox scats were collected in the alpine zone in November because, with melting snow still on the transect, their date of deposition (winter or spring) could not be ascertained. Bogong moth remains in scats peaked in January, thereafter there was a general decline during February (which at the Thredbo Automatic Weather Station has the highest mean maximum and minimum temperatures and is also the driest month). After February, bogong moths were not common in scats at subalpine altitudes but increased in frequency in scats at alpine altitudes (Fig. 3)

Temperature

At Charlotte Pass (1755 m asl), over the period November 2009 to March 2010, the average temperature in the boulder field $(12.3\pm2.9^{\circ})$ was not significantly different (t= 0.787, df=118, p=0.433) from that in the Bureau of Meteorology Stevenson Screen $(12.2\pm3.4^{\circ})$. However, at the South Ramshead site (1950 m asl) over the period December to March, the temperatures in the cave and Stevenson Screen were significantly different in both 2002/03 (t= 2.849, df=95, p<0.01) and 2003/04 (t= 4.692, df=106, p<0.0001). Though significant, this may not be biologically important with the temperature in the cave differing little from that in the Stevenson Screen in 2002/03: $11.9\pm3.5^{\circ}$ against $12.2\pm4.4^{\circ}$, and in 2003/04: $10.7\pm3.6^{\circ}$ against $11.2\pm4.3^{\circ}$. Corrected for a temperature lapse rate of 0.77 °C per 100 m (Galloway 1988), these differences would be equal to a difference in altitude of 40 and 65 m respectively.

Over the period November 2009 to March 2010, there was a significant difference (t= 16.843, df=104, p<0.0001)) between temperatures at the Charlotte Pass Stevenson Screen ($12.3\pm3.5^{\circ}$), and the bogong moth

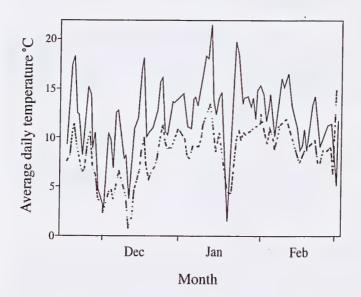


Fig. 4 Average daily temperatures over the period November 2009 to March 2010 in the Bureau of Meteorology Stevenson Screen at Charlotte Pass, 1755 m (solid line) and the bogong moth aestivation site on Mt Kosciuszko, 2210 m (broken line).

aestivation site on Mt Kosciuszko at 2210 m asl ($8.6\pm2.5^{\circ}$). Although these were significantly different, the plot of the two locations suggests that the two were following the same general weather patterns (Fig. 4), with differences mainly related to the air temperature lapse rate. In fact, when all locations were plotted there was a highly significant negative relationship between average temperature and altitude ($r^2 = 0.943$, p<0.0001) (Fig. 5), and the expression (0.0068x) in the equation of the line y = -0.0068x + 24.278 closely approximated the expected lapse rate of 0.0077x where x is the altitude in metres (Galloway 1988).

The winter temperatures showed differences between sites among rock tors on the South Ramshead and in boulderfields on the flanks. In the period leading into the full winter snowcover, the sites fluctuated in reasonable synchrony (Fig. 6). However, once the snowcover blanketed the boulderfields the air space between boulders was disconnected from the ambient air and in the second half of winter there was no fluctuation in the temperature trace.

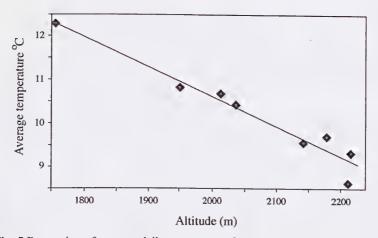


Fig. 5 Regression of average daily temperature from November 2009 to March 2010 in bogong moth aestivation sites on altitude. The formula of the line is y = -0.0068x + 24.278.

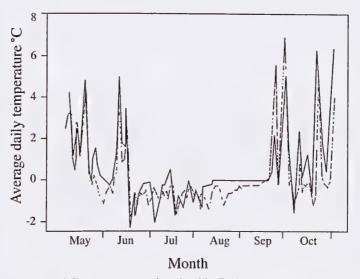


Fig. 6 Average daily temperatures in a boulderfield at 1950 m (solid line) and rock tors at 2015 m (broken line) on the South Ramshead over the period when obligate parasites of bogong moths are independent of their hosts

By contrast, because of the architecture of the upright boulders in the tors, there was no such disconnection in the sites in these tors. Summer temperature data from the north and south aspects of the South Ramshead and Mt Townsend showed opposite trends. For South Ramshead, the bogong

moth caves on the northerly aspect were warmer $(10.7\pm3.5^{\circ})$ than the south facing caves $(10.4\pm3.4^{\circ})$, a significant difference (t= 2.200, df=104, p<0.05). By contrast, for Mt Townsend the bogong moth caves on the southerly aspect were warmer $(9.5\pm3.1^{\circ})$ than the north facing caves $(9.3\pm3.4^{\circ})$, again a significant difference (t= 2.174, df=104, p<0.05). However, there were slight altitudinal difference between the sites on north and south (80 m for Mt Townsend and 25 m for the South Ramshead) and when this was corrected for using a lapse rate of 0. 77^{\circ} per 100 metres (Galloway 1988), there was no significant difference between aspects on the South Ramshead (t= 433, df=104, p= 0.666) whereas on Mt Townsend the northerly aspect was significantly warmer than the south (t= 5.301, df=104, p< 0.0001).

Relative humidity

Over the period November 2009 to January 2010, there was a significant difference (t= 3.621, df=51, p<0.001) between mean daily relative humidity at the Charlotte Pass Stevenson Screen ($64.5\pm15.2\%$), and the boulderfield moth aestivation site at the same location ($70.2\pm17.3\%$). Over the period November 2009 to March 2010, there was a significant difference (t= 11.738, df=71, p<0.0001) between mean daily relative humidity at the Charlotte Pass Stevenson Screen ($66.7\pm14.2\%$), and the moth aestivation sites at Mt Townsend ($75.9\pm14.4\%$), a similar figure to that recorded on the South Ramshead northerly aspect cave from November 2001 to March 2002 ($75.3\pm14.4\%$).

Discussion

Distribution

The apparently suitable but unoccupied rock outcrops on the Crackenback Range may reflect a preference by bogong moths for higher, cooler sites, even though moths were found elsewhere at lower altitudes such as at about 1200 m on the north side of Mt Tingaringy. However, it might also be possible that along the length of the Crackenback Range, until South Ramshead is reached, most of these sites have rolling terrain to the north and west and the outcrops are not distinct landmarks except from the south. If moths find the sites visually these might not stand out on dark nights. The whole question of how bogong moths find their chosen sites and the roles and relative importance of visual and olfactory cues is one that requires some attention.

Common (1954) found large aggregations on south-western slopes and none on apparently suitable sites on north-easterly slopes, and Blakers (1980) suggested that aestivation sites were preferentially located on the south side of peaks. Common (1954) did speculate that the chosen aspect in the Brindabellas may be a result of the availability of outcrops and the present study showed that throughout the Snowy Mountains overall, there was no fixed aspect on which bogong moths congregated. The location of aestivation sites and camps was more a result of geomorphology than choice of aspect. The preference for higher sites, when available, appears to occur seasonally, where through incremental upwards movement, or because more room becomes available due to attrition of populations over the summer period through mortality or migration, moths moved to higher aestivation sites particularly from February onwards.

Numbers

There has been little information on the summer distribution of bogong moths in the past, outside of the Brindabella Range (Common 1954). The difficulties in calculating total numbers in aestivation sites from the unknown proportion that are visible, means that there have been no attempts to date to calculate a total number of bogong moths migrating annually. From a process of allocating mortality between predation, parasitism and weather-related mortality, Green (2010) calculated a total mortality of 985 million bogong moths in the Snowy Mountains annually. Blakers (1980) estimated that in a 'good year' for moth numbers there would be a 45% reduction in numbers of bogong moths while in aestivation sites. Based on this, a first order estimate of the number of moths migrating to the Snowy Mountains annually would be 2.2 billion. Allowing for early season mortality of about 285 million moths, when moths were mainly occupying camps (Green 2010), the estimated number of bogong moths in the Snowy Mountains at its peak (around 1 January, see Common 1954), would be about 1.9 billion moths. At a density of 17 000 moths m⁻² (Common 1954) this would require 112 000 m^2 of usable rock face in the main aestivation sites at peak abundance. If these were spread evenly across the 42 aestivation sites recorded here, there would be about 45 million moths per site. On the wall of Common's observation cave were an estimated 144 000 moths (Common 1954). Bennett (1834) stated that, 'the quantity of moths which may be collected from one of the granite groups, it is calculated would amount to at least five or six bushels' (180-220 litres). This would translate to about 200 000 moths at 100 per litre. These are the figures for the easily observed (and captured) numbers and represent less than half a percent of the total calculated per site. These easily counted moths, that by definition occupy the most exposed, and possibly least preferred areas of suitable wall (Common 1954) would probably not be of great value in calculating numbers of the unknown proportion within aestivation sites. Hence the difficulties in calculating annual variation in total numbers of migrating moths appear to be intractable at present.

Temperature and relative humidity

Crevices in tors and boulder fields act like dynamic caves, that is, air flows through them as part of the general air circulation with almost instantaneous warming and cooling (Geiger 1965; Harris and Pedersen1998). This was demonstrated for a cave on the South Ramshead, where comparisons between logger temperatures in the boulders followed temperature recorded in a nearby Stevenson screen differing only by 0.3° through summer of 2002/03 and 0.5° in 2003/04. At the Charlotte Pass boulder fields the match was much closer (0.1°). There will be a varying relationship between measured temperatures, perhaps dependent on the exact placement of the loggers that cannot be standardized in the same way as measurements in a Stevenson screen. Regardless of this, as temperatures fell with altitude so did the temperatures in aestivation sites, and at about 0.7° C per hundred metres of ascent it fell at close to the lapse rate calculated by Galloway (1988).

More uniform temperatures and higher humidity are characteristic of caves (Geiger 1965). Relative humidity in caves in the present study also changed with the general air circulation patterns, rising and falling with that recorded in a meteorological screen. However, the relative humidity in caves was about 10% higher in moth aestivation sites. This would probably be higher still where the moths congregate, overlapping like tiles and further restricting moisture transport to the circulating air (Common 1954). This could be important in reducing water loss by the moths during aestivation because, when moths, en masse, leave the caves to drink they may be more exposed to predators (Green pers.obs.).

Climate change

Concerns have been expressed as to the impacts of climate change on bogong moths and their predators, particularly the mountain pygmy-possum (Burramys parvus) (Heinze et al. 2004). The major predators on bogong moths in the Snowy Mountains are little ravens (Corvus mellori), bush rats (Rattus fuscipes), Richard's pipits (Anthus novaeseelandiae) and foxes (Vulpes vulpes) (Green 2010). Although not an important predator on the moths, B. parvus is the only predator that is dependent on them, in fact, high altitude populations of B. parvus would not survive without access to migratory bogong moths as a food resource (Heinze et al. 2004). Two species of mermithid worms that parasitise bogong moths Amphimermis bogongae and Hexamermis cavicola (Welch 1963) are also dependent on them (Common 1954). These worms emerge from the moths in January and February, causing their deaths. They remain in the caves over winter and reinfest moths in spring. For these species that remain in the moth sites, the wintering temperature is also important. In this case the temperatures in the two architectures (boulderfields and caves in tors) do not correspond as well as they do in summer. Initially, after the moths have left, temperatures are similar but as snow begins to accumulate they become disconnected, and with full snowcover the winter temperature in the boulderfields is fully disconnected from ambient temperature fluctuations and remains steady at just above 0°C (Fig. 6) while the caves in tors still maintain a connection with outside temperature because of the upright, more open, architecture. This, however, may have little impact on the overwintering worms if they are

buried deep in the moth detritus on the floor of caves, and *B. parvus* is unlikely to remain in the caves in tors over winter, probably leaving for lower altitude boulderfields once the moths have gone.

Migration accompanied by diapause may be essential for the survival of bogong moths (Common 1954). Without the refuges in boulderfields and caves, this may not be possible. The present study shows that while the bogong moths occupy the highest possible altitude within their range, and there is an upward movement through the summer season as conditions become warmer and drier, there is still some flexibility because it is the lowest altitude that they can occupy that is important in determining their requirements. While loss of some lower altitude sites may have an impact on the numbers that can aestivate, the loss of progressively higher sites with climate warming will take some time. There will be a varying relationship perhaps in different locations between temperature inside and outside of aestivation sites but, as global temperatures rise so, obviously, will the temperatures in boulderfields. Because the aestivation sites generally follow air temperature they will become unusable at the same rate as regional warming so that a worst case scenario of warming in alpine areas of 2.9°C by 2050 (Hennessy et al. 2008) will lead to a loss of aestivation sites in the lowest 400 m of their range unless moths are able to adapt. Taking the Mt. Tingaringy site (1200 m) as a possible minimum altitude for aestivation, means that most sites above 1600 m should still prove suitable for aestivation and this includes all of the sites recorded in the present study.

Conclusion

Crevices among boulderfields and rock tors provide a dark, cool, relatively stable and moist environment necessary for aestivation and the long-term survival of bogong moths in high numbers. The locations where moths congregate are far enough from the outer surface of the rocks for aspect not to be important. Because the temperature in aestivation sites is dependent on shade air temperature, higher sites are cooler in accord with the regional temperature lapse rate. Most sites used in the Snowy Mountains are above 1700 m altitude and even in a worst-case climate change scenario to 2050 should be proof against becoming unsuitable for moths.

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